



On the discovery of a new polymorphic Happy-Face Spider (Araneae, Theridiidae) from the Western Himalayas, India, with notes on its natural history

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Abstract

A new species of *Theridion* is reported here from Uttarakhand, India which resembles and exhibits polymorphism like the Happy-face spiders reported from the Hawaiian Islands, *Theridion grallator*. The species is polymorphic in both sexes and exhibits patterns of a smiling face with dots in colours of red, black and white arranged differently. 32 different morphs of the species have been reported here which have been collected from three different locations in the northwestern state of India, Uttarakhand. This *Theridion* species also builds webs to hang upside down like the other polymorphic spiders *T. californicum* and *T. grallator*. The phylogenetic position of the species is also reported here which was compared against some of the Asian and Neotropical species across the world using the COI marker. A genetic variation of around 8.5% is observed from the Hawaiian Happy-face spider which indicates a separately evolved species in Asia where several morphs have been found. Despite moderate overall divergence, *T. himalayana* appears to be phylogenetically isolated from both its Palearctic and Nearctic congeners. This supports its distinctiveness within the genus and raises broader questions about lineage dispersal, parallel evolution of colour polymorphism and independent evolution of species in montane forests. A dichotomous key to the *Theridion* species described from India is also presented here.

Key Words

Happy-face spider, polymorphism, dichotomous key, Phylogeny, Theridiidae, Uttarakhand, India

Introduction

The discovery of polymorphic spiders in the Hawaiian Islands marked a milestone in evolutionary biology, offering a vivid example of parallel evolution and phenotypic diversity within a single lineage. These spiders, particularly from the genus *Theridion*, fascinated researchers with their striking colour morphs and ecological versatility, thriving on different plants in the same habitat. Polymorphism, as it is termed, has fascinated ecologists worldwide, who seek to understand the genetic mechanisms underlying such expression.

By the turn of the 20th century, after the discoveries of *Theridion grallator* (Simon, 1900) and *Enoplognatha ovata* reported by Oxford (1985), other polymorphic spiders were discovered, from different parts of the world like *Theridion californicum* (Oxford, 2009), *Selkirkella alboguttata* (Cotoras et al. 2017), and *Spintharus* (Agnarsson, 2019).

As an intriguing discovery, our recent fieldwork in the Indian Himalayas has uncovered a spider species exhibiting polymorphic traits from the genus *Theridion* (Walcknaer, 1805). Here, we present the morphological, ecological, and phylogenetic data for this Himalayan polymorphic spider which distinguishes it as a different species from the others reported to date.

Background

The genus *Theridion* (Walckenaer, 1805), contains 577 described species, more than one-fifth of all Theridiidae spiders found worldwide (World Spider Catalog 2025). The Theridiidae family is vast and diverse mostly known for several significant traits in different genera like matrophagy, cannibalism and kleptoparasitism (Agnarsson 2004). Because of their sheer diversity and size, few genera like *Theridion* have been proposed to be further grouped into smaller species-groups by Levi (1957). Forster et al. 1990 suggested that the genus *Theridion* has typically been used to shelter species broadly classifying on the absence of the colulus only. At present, India has reports of six species under the genus *Theridion* with *Theridion odisha* as its latest addition reported by Prasad et al. (2019) from Bhubaneswar, Odisha. This extremely diverse genus therefore requires more revision to delineate species with common traits in a more discrete manner. Further this family's diversity and evolution have been less explored in India.

Theridion grallator, also called the Hawaiian Happy-face spider, was discovered by Simon (1900) from the Hawaiian Islands, United States. The etymology 'Happy-face spider' stems from the presence of a smiling face like an archetype on its abdomen. It was reported that this spider has multiple morphs of similar smiling patterns reported from different locations of the islands of Hawaii (Gillespie and Tabashnik 1990) in the same species. Polymorphism has been reported in other spiders besides *T. grallator* such as *Theridion californicum* (Oxford, 2008), *Enoplognatha ovata* (Oxford 1983; Oxford and Gillespie 1996) and *Spintharus* (Agnarsson, 2019). However, the typical smiling face pattern is specific only to a few species. *Selkirkiella alboguttata* (Cotoras et al. 2017: fig. 2D) has been reported to have a 'red front' pattern but we consider it to vary considerably from the smiling face archetype described in the present study. During faunistic surveys in Chamoli and Rudraprayag district of Uttarakhand, India, we came across a similarly patterned new species of Happy-face spider from the Himalayan moist temperate deciduous forests of India. The distribution map of the different polymorphic species in the Theridiidae family is shown in the map at Fig. 1. The *Theridion* species described from India are marked in Fig. 2 along with the site of the new species described here.

Materials and methods

The sampling design includes 16 nos. of 100 m x 50 m plots distributed in the Himalayan moist temperate deciduous forest. The collection was carried out from April to October of 2023 and 2024. Specimens were collected using direct capture, bush beating, pitfalls, and sweeping per plot. Specimens were preserved in 70% ethanol.

Specimens were sorted and identified under a Stereomicroscope (Zeiss Stemi 2000C). Photography was done

using a camera attached to a Leica stereomicroscope M205A, using the software Leica Application Suite v. 4.4. Both the male pedipalp and the female epigyne were excised with the help of entomological needles to facilitate observation under the scope. The muscle tissue of the epigyne was further removed with the needles and digested using immersion in potassium hydroxide (KOH) at 30% concentration. For FESEM and SEM images, palps were excised and cleaned ultrasonically for one minute and then transferred to 100% ethanol overnight. Palps were submitted to dehydration using 100% ethanol for further drying, glued to flat-headed rivets and gold sputter-coated. Imaging was conducted with the help of a Quanta 200 environmental SEM. Images were edited and measured using Adobe Photoshop 2021 and ImageJ v. 1.53e. Maps were prepared using SimpleMappr (<https://www.simplemappr.net/>).

Morph assortment

A total of 61 individuals were analysed in this study. These represented an expansion from 32 illustrated morph records by incorporating their observed field frequencies. Specimens were collected from three localities—Makku (m), Tala (T), and Mandal (M)—and preserved individually in Eppendorf tubes containing 70% ethanol. The dataset comprised 24 males (39.3%) and 37 females (60.7%), and included 40 juveniles (65.6%) and 21 mature individuals (34.4%).

The specimens were segregated into two categories, 'mature' and 'juvenile' based on the presence or absence of developed genitalia structures. The juveniles in general were found to have pale body colour and smaller legs. Although it was not possible to sex juveniles distinctly at very early stages, we attempted to identify juvenile females from males by looking at the palp structure (bulbous) and epigynal region (elevated epigynal area). Establishing structures to segregate sexes in juveniles is yet to be done, hence we cannot consider the same as a taxonomic trait yet as it will depend on the specific moult/stage of life of the individual (depicted in Suppl. material 4).

In the laboratory, each specimen was examined under a stereo zoom microscope (Leica S9i), and its abdominal morph was manually illustrated on white paper. As additional specimens were processed, newly observed morphs were compared with existing sketches and catalogued along with sex, life stage, and collection site information.

All hand-drawn illustrations were photographed, and each morph was isolated by cropping, resulting in 32 distinct morphs (Fig. 11). These were then digitized and coloured in Adobe Photoshop according to their natural colour patterns. Though the total number of morphs was 32, we created discrete groups because several morphs lacked clear boundaries and exhibited partial overlap in pattern characteristics. Therefore, five major morph groups were established, within which morphs sharing similar pattern features were combined (Table 1).

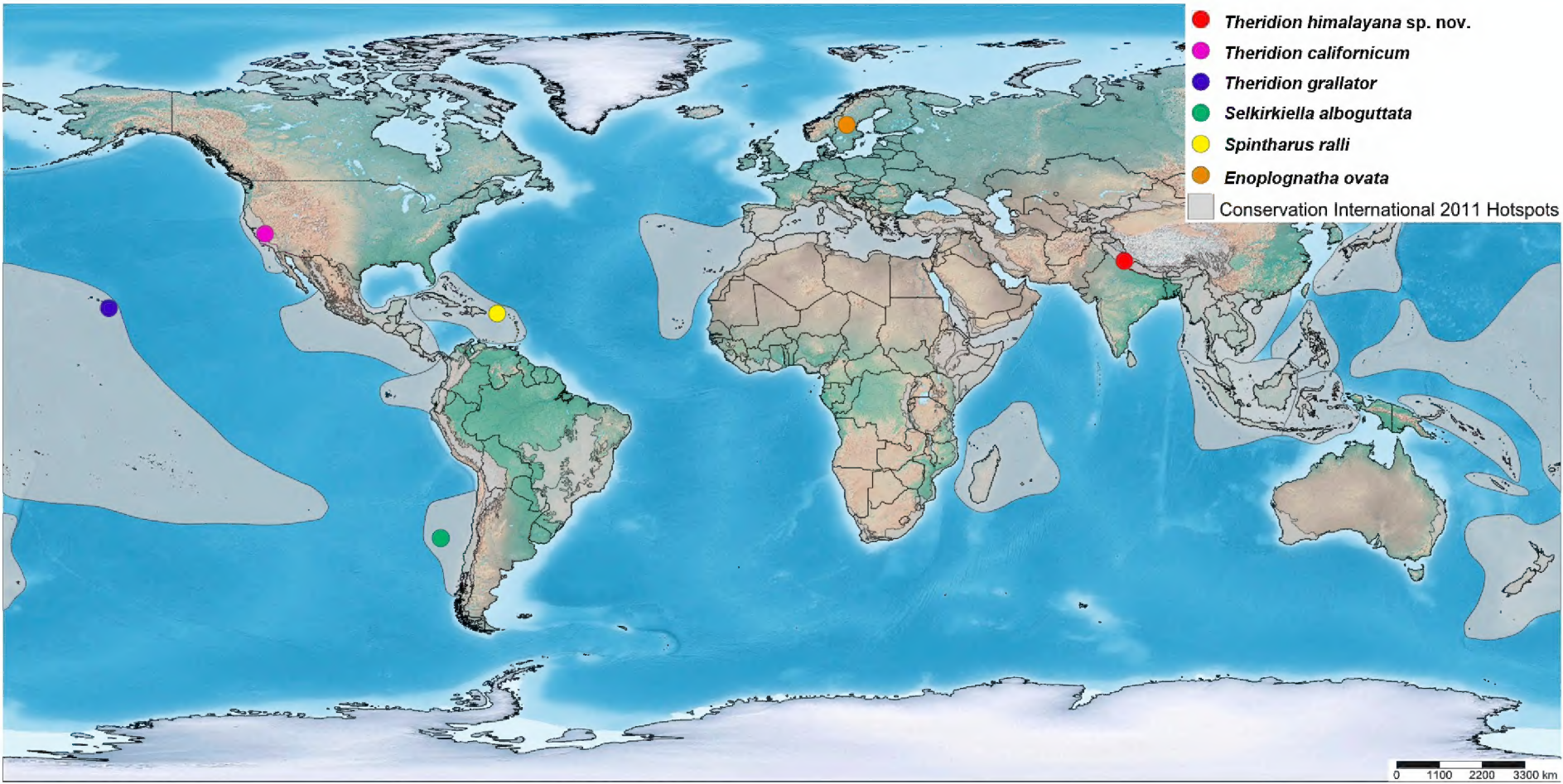


Figure 1. Map showing spiders in family Theridiidae exhibiting polymorphism across the world with the newly described species from the Himalayan region.



Figure 2. Map showing the *Theridion* spp. from India with the locality record of the newly described *Theridion himalayana* sp. nov.

After the grouping, collages were prepared based on site, sex, and major morph categories.

Each morph was assigned a unique three-letter code (“__”). The first position denotes sex (M for male, F for fe-

male), the second denotes maturity (J for juvenile, M for mature), and the third represents the morph identifier (A, B, C, D, ...). For instance, the code **MJD** refers to the fourth morph, corresponding to a juvenile male (Suppl. material 5).

Morph classification system

Statistical methods

To examine associations among sex, life stage, morph type, and collection site, contingency table analyses were performed using chi-square tests and Fisher’s exact tests where appropriate. Effect sizes were calculated using Cramér’s V statistic. Statistical significance was assessed at $\alpha = 0.05$. All analyses were conducted in PAST software.

(MCMC) chains were run for 2 million generations with sampling every 1000 generations, discarding the first 25% as burn-in. Convergence was assessed using split frequency diagnostics and effective sample size (ESS) values in Tracer v1.7.2. Maximum likelihood (ML) phylogeny was reconstructed using IQ-TREE v2.2.2, implementing the same substitution n model (GTR+I+G) with 1000 ultrafast bootstrap replicates to assess node support. Trees were visualized and edited in FigTree v1.4.4. Pairwise uncorrected p-distances

Table 1. Classification of morph patterns found on the polymorphic spider *Theridion himalayana* sp. nov. into five major groups.

Code	Morph group	Full Description	Characteristics
A	RBWR	Red Blob White Ring	Red pigmentation with white reflective ring (guanine deposits)
B	RBBR	Red Blob Black Ring	Red pigmentation bordered by black/dark pigmentation
C	PB	Planarian Base	Pattern resembling planarian flatworm (linear/bilateral striping)
D	NPB	Non-Planarian Base	Baseline unpatterned yellow/cream opisthosoma without planarian pattern
E	WR	Whole Ring	Continuous ring pattern around opisthosoma perimeter

Phylogeny

For molecular analysis DNA was extracted using two to four legs of the spider specimen. The Qiagen™ Tissue kit was used for extraction and after visualising the amount, the samples were amplified for the COI gene using the Chelicerate primer with a PCR with standard thermocycler conditions (the primer details are as given in Table 2). The PCR product was purified using a QIAGEN PCR purification kit and was sent for sequencing at HereditY Life Sciences Pvt. Ltd., Bhubaneswar. <http://iqtree.cibiv.univie.ac.at/>) to estimate the best model of sequence evolution using a Bayesian Information Criterion (BIC) and subsequently generated a Maximum Likelihood tree. The best-fit nucleotide substitution model was determined using Modelfinder, implemented in IQ-TREEv2.2.2, under the Bayesian Information Criterion (BIC).

Cytochrome C Oxidase subunit I (COI) sequences (Suppl. material 1) representing 44 species from the spider family Theridiidae—including members of *Theridion*, *Coleosoma*, *Meotipa*, *Parasteatoda*, *Chryso*, *Rugathodes*, *Exalbidion*, *Theridula*, and *Ameridion*—were analyzed. Two non-*Theridion* theridiids (*Steatoda paykulliana* and *Argyrodes argentatus*) were used as outgroup taxa (Suppl. material 2). All sequences were aligned using MAFFT v7.475 with default parameters. Ambiguously aligned or poorly conserved regions were manually inspected and trimmed. Bayesian phylogenetic inference was carried out using MrBayes v3.2.7a under the GTR+I+G nucleotide substitution model. Four Markov chain Monte Carlo

were calculated from the trimmed COI alignment using the dist.dna() function in the ape package in R v4.1.1. The resulting distance matrix was visualized both as a heatmap using heatmap and as a hierarchical cluster dendrogram using the hclust() and as.dendrogram() functions from the stats package.

The holotype specimens have been deposited at Zoological Survey of India (ZSI), Berhampur, Odisha, India and paratypes have been deposited at ZSI, Berhampur, Odisha, India and Regional Museum of Natural History (RMNH) Bhubaneswar, Odisha, India. The description of the new species followed the format of Vanuytven (2021). All measurements are in millimetres. The GPS coordinates of the collection localities were taken with the help of a Garmin GPSMAP 66S (Datum WGS 84).

Abbreviations used in the text: **AER** – anterior eye row; **ALE** – anterior lateral eye; **AME** – anterior median eye; **EFL** – eye field length; **PER** – posterior eye row; **PLE** – posterior lateral eye; **PME** – posterior median eye; **RTA** – retrolateral tibial apophysis; **ESOs** – External Sense Organs; **FE-SEM** – Field Emission Scanning Electron Microscopy; **SEM** – scanning electron micrograph; **PMS** – Posterior Median spinneret; **ALS** – Anterior Lateral Spinneret; **PLS**-Posterior Lateral Spinneret; **MAP**– major ampullate gland spigot; **PI**– piriform gland spigots; **mAP**-minor ampullate gland spigot; **AC** – acini-form gland spigots; **CY** – cylindrical gland spigot; **ST** – subtegulum; **T**-tegulum; **TC** – tarsal comb; **TTA**-theridiid tegular apophysis; **C** – conductor; **CD** – copulatory duct; **CO** – copulatory opening; **E** – embolus; **FD** – Fertilization Duct.

Table 2. List of primers used in the study.

Target	Primer Name	Direction	Sequence	Reference
COI	LCO 1490	Forward	5'-GGTCAACAAATCATAAAGATATTGG-3'	(Miller et al. 2013)
COI	Chelicerate Reverse 1	Reverse	5'-CCTCCTCCTGAAGGGTCAAAAATGA-3'	(Barret and Hebert 2005)

Results

Taxonomy

Genus *Theridion* Walckenaer, 1805

Type species. *Theridion himalayana* Priyadarshini and Tripathy, sp. nov.

***Theridion himalayana* Priyadarshini & Tripathy, sp. nov.**
<https://zoobank.org/0E9B7A9E-BBFF-4835-941C-D62D1DF14FA8>

Type material. *Holotype* ♀ (ZSI/EBRC/Ar-18540), from India: Uttarakhand, (30.473531°N, 79.1696°E), 2207.15 m above sea level, 06.8.2024, Coll. A. Tripathy.
Paratypes: 2 ♀ (ZSI/EBRC/Ar-18541) data same as holotype, 15.8.2024.

Etymology. The specific epithet ‘*himalayana*’ is assigned to species owing to the locality from which it was first found as an ode to the mighty Himalayan Mountain range that holds a wealth of biodiversity.

Suggested common name. Himalayan Happy-Face Spider.

Diagnosis. *Theridion himalayana* sp. nov. can be readily distinguished from other Indian congeners by the unique configuration of the copulatory ducts (CD) and fertilisation ducts (FD). In *T. himalayana* sp. nov., the CD is elongate, strongly curved, and prominently protruding forward, with both ducts running almost parallel before terminating downward. The CD which is longer than the spermathecae exhibits a distinctive sew-hook-like appearance,

which is not observed in any other examined species. The fertilisation ducts are short, narrow, and directed upwards, diverging away from each other to form a V-shaped orientation. The FD arises below the spermatheca, with each duct directed opposite to the CD. This configuration clearly separates *T. himalayana* sp. nov. from *T. odisha*, which has a S-shaped, coiled CD that terminates in oval loops and FD inclined towards each other; *T. bengalensis*, where CD is short, slender, and directed away from each other, while FD appears tapering distally and directed away from spermatheca; *T. melanostictum*, characterized by extremely long, highly coiled CD and downward-directed, sickle-shaped FD; *T. zonulatum*, which possesses short, uncoiled CD and looped FD directed upwards.

Theridion himalayana sp. nov., which resembles *Theridion grallator* the most with respect to general morphology and colour pattern, can be easily distinguished apart by the structure of genitalia of both male and female individuals. *T. grallator* has short, curved CD which converges only at the opening and a FD that runs parallel to the spermathecae whereas the combination of hook-shaped, downward-terminating copulatory ducts and short, upward-directed fertilisation ducts is diagnostic for *Theridion himalayana* sp. nov. Although genitalia were found not to be similar, morphology of the spider along with abdominal patterns came closest to *T. grallator* as none of the other congeners exhibited polymorphism. A detailed comparison of genitalia and related characters has been presented in the table below (Table 3).

Description. Female (holotype).

Measurements. Total length – 2.94 mm, Carapace length – 1.17 mm, width – 0.94 mm. Abdomen length – 1.77 mm, width – 1.00 mm, Leg I – 3.47/0.44/2.84/4.24/0.89,

Table 3. Comparative diagnosis of genitalia characters in different *Theridion* species.

Species vs. Character	CD	FD	CD – Spermatheca	Genitalia shape	CD opening	FD – CD direction	Morph No.s
<i>Theridion himalayana</i> sp. nov.	CD is curved protruding into a hook shape facing each other and parallelly terminates downwards	FD Short directed upwards away from each other making a V shape	CD longer and protruding	Sew hook type	Below the spermatheca facing downwards	Directed in opposite direction	30+
<i>Theridion odisha</i>	CD is long and ‘S’ shaped terminating in an oval loop	FD short directed upwards and inclined towards each other	CD longer and coiled in S shape	Frog faced	Facing each other making an oval loop	Directed parallel to each other	0
<i>Theridion bengalensis</i>	CD small, slender and directed away from each other	FD is short broader at base and tapering towards the tip.	CD is shorter than spermatheca	Kidney shaped	Opening not facing each other towards opposite sides	FD directed away from spermatheca	0
<i>Theridion melanostictum</i>	CD very long and highly coiled.	FD relatively shorter directed downwards with sickel shaped tip	CD very long and spermatheca very small	Highly coiled	Directed towards each other	Oriented in same direction	0
<i>Theridion zonulatum</i>	CD short facing downwards without coiling	Small directed upward making a loop	CD smaller than spermatheca	Club shaped	Opening downwards directed towards each other	Oppositely downwards	0
<i>Theridion grallator</i>	CD short curved and directed downwards converging at the opening	FD directed downwards parallel to spermatheca	Spermatheca longer	Bow tie type	CD opening faces downwards	Directed in same direction	20+

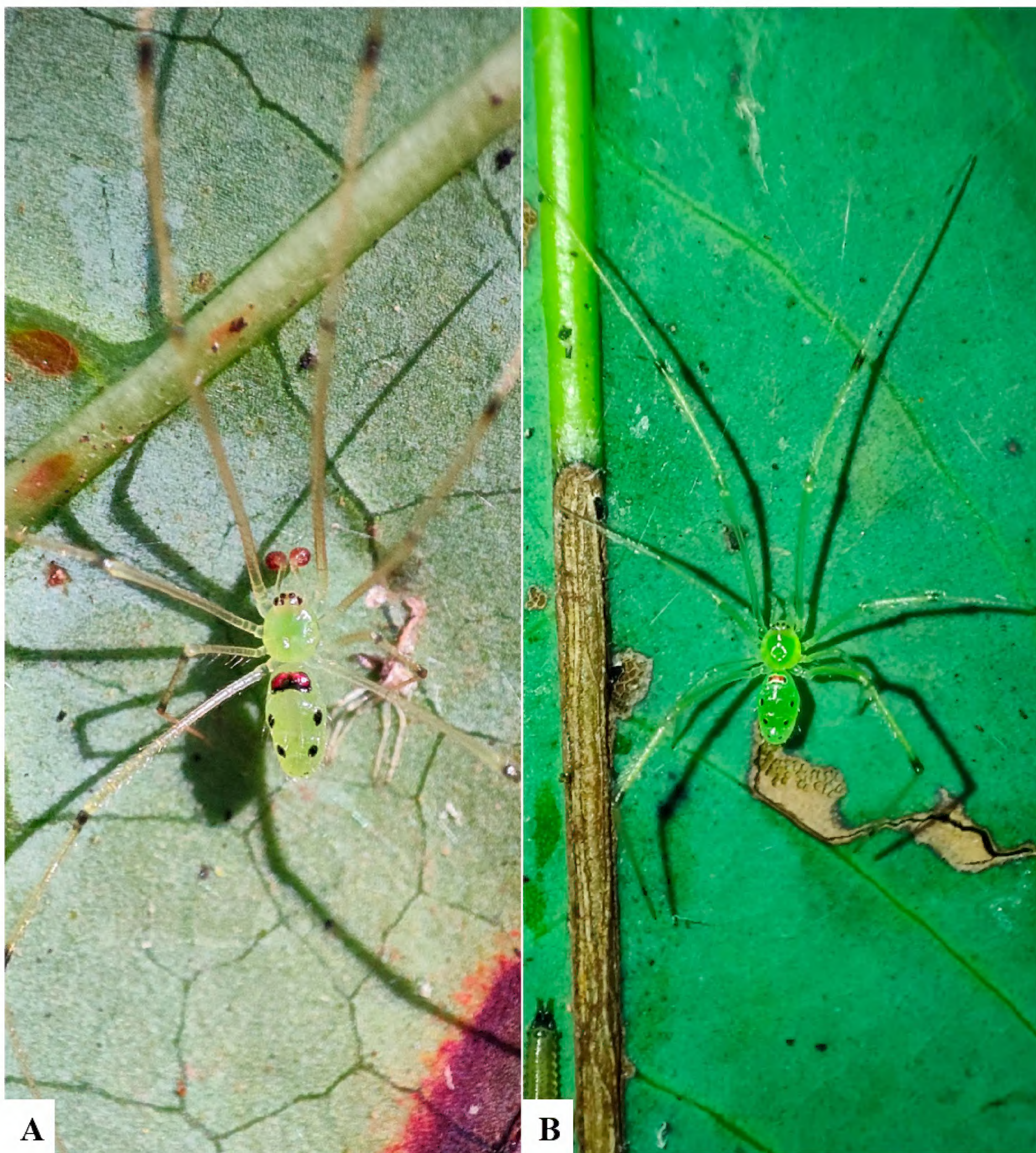


Figure 3. Habitus of live male (A) and female (B) *Theridion himalayana* sp. nov.

Leg II – 2.32/ 0.31/1.54/2.15/0.70, Leg III – 1.42/ 0.30/0.82/1.19/0.49, Leg IV – 2.92/0.38/2.05/2.77 /0.70.

Small-sized, greenish-yellow spider (Fig. 3B).

Cephalothorax: Carapace translucent yellow with radiating green hues from the centre with a minor fovea (Fig. 4). Clypeus and chelicerae are clear without any markings. AME, PME, ALE and PLE are all the same size and diameter (Fig. 4A). Fangs brown and smooth (Fig. 4B) In lateral view, the cephalothorax is flat, eye region raised as depicted in Fig. 4C. Dorsally, the eye

region is surrounded by 9 setae i.e., 2 between PME and AME, 1 on each side between the PLE and PME, 2 posterior to PLE on each side and 1 present distally between the PME. This combined forms an elliptic ring like arrangement (Fig. 5B). Also, a 5 setae arrangement distally to the elliptical arrangement in the centre of the cephalothorax and anterior to the fovea is present.

Abdomen: In lateral view, flat from the dorsum and rounded with a red blob in the anterior dorsum surround by a white ring. Distally five black spots surrounded by

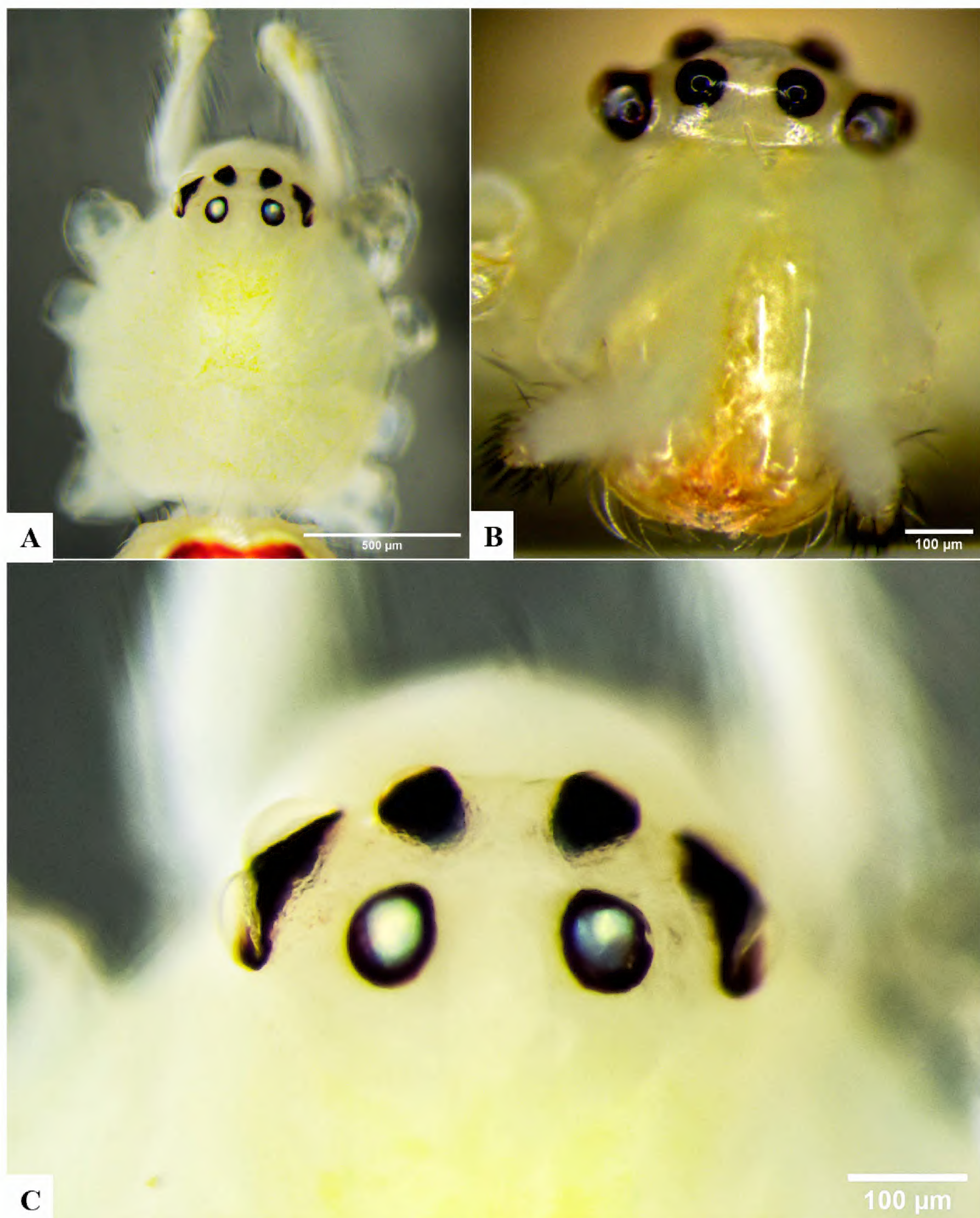


Figure 4. **A.** Cephalothorax of female holotype of *T. himalayana* sp. nov.; **B.** Showing the eye, chelicera, and the fangs; **C.** Showing the eyes of the female.

white spots in a ‘V’ shape are present (Fig. 5A). Laterally covered with more pronounced white hairs than the ventral and dorsal region (Fig. 5B).

Epigynum: Loop like rounded in structure, small, like ‘Sew Hook’ shape (Fig. 5C, E). Copulatory duct longer than spermatheca length. External genitalia protruding

flap like overhanging on a minor depression in the epigynal region (Fig. 5D). Spermatheca oval and slightly tapering posteriorly at the junction of CD (Fig. 5F, G).

Legs: Legs slender, translucent, light yellowish, straw coloured with black to brown, discrete rings on femora, tibia distally brown, metatarsus apically

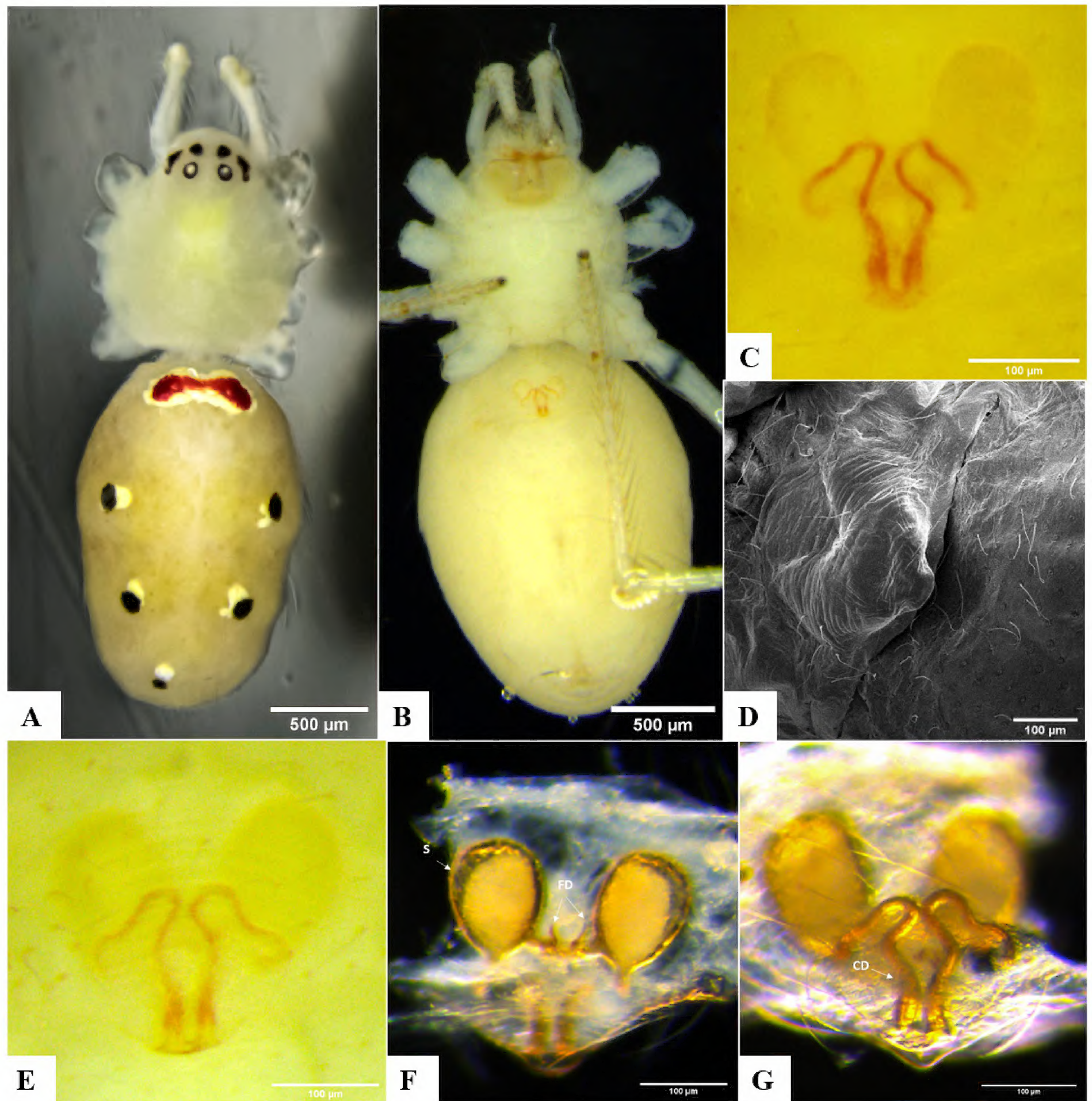


Figure 5. *T. himalayana* sp. nov. female **A.** Habitus dorsal view **B.** Habitus, ventral view of the holotype **C.** External female genitalia of holotype **D.** SEM micrograph of external female genitalia; **E.** External female genitalia of a different morph; **F.** Internal genitalia showing the spermatheca (S) and the fertilisation duct (FD); **G.** Showing the copulatory duct (CD).

darker (Fig. 6A). The first and fourth pair of legs have black spots at the tarsal – tibial and femur-tibia joints, where the one between tibia and metatarsus is most prominent while the rest are faintly visible. The other two legs also have similar black marks but are sometimes absent or very faint.

Leg Formula: I > IV > II > III

Spinnerets: Spinnerets same as body colour, light yellowish white protruding outwards from abdomen. Not very distinct in colour but raised from the surface of the abdomen; Arrangements of spigots on ALS, PMS, PLS like that of other Theridiinae (Fig. 7A–F). About 35–40

piriform spigots (PI) on ALS (Fig. 7D). One cylindrical spigot on PMS (Fig. 7C) each with short base. Flagelliform spigot on PLS longer than its cylindrical spigot length. Two acini-form spigots on PMS. Shaft of minor ampullate spigot longer than cylindrical spigot on PMS.

Sensilla: Six sensillar structures were present on all the legs namely trichobothria, mechano-sensory setae, lyri-form organ, slit organ and trichoidea sensilla (Fig. 8A–E). The tarsal organ was only found on the pedipalp of the male. Tarsal comb with elevated base, straight serrations, distinctly notched (Fig. 6C, D) typical to that of Theridiinae (Agnarsson 2004) was reported.

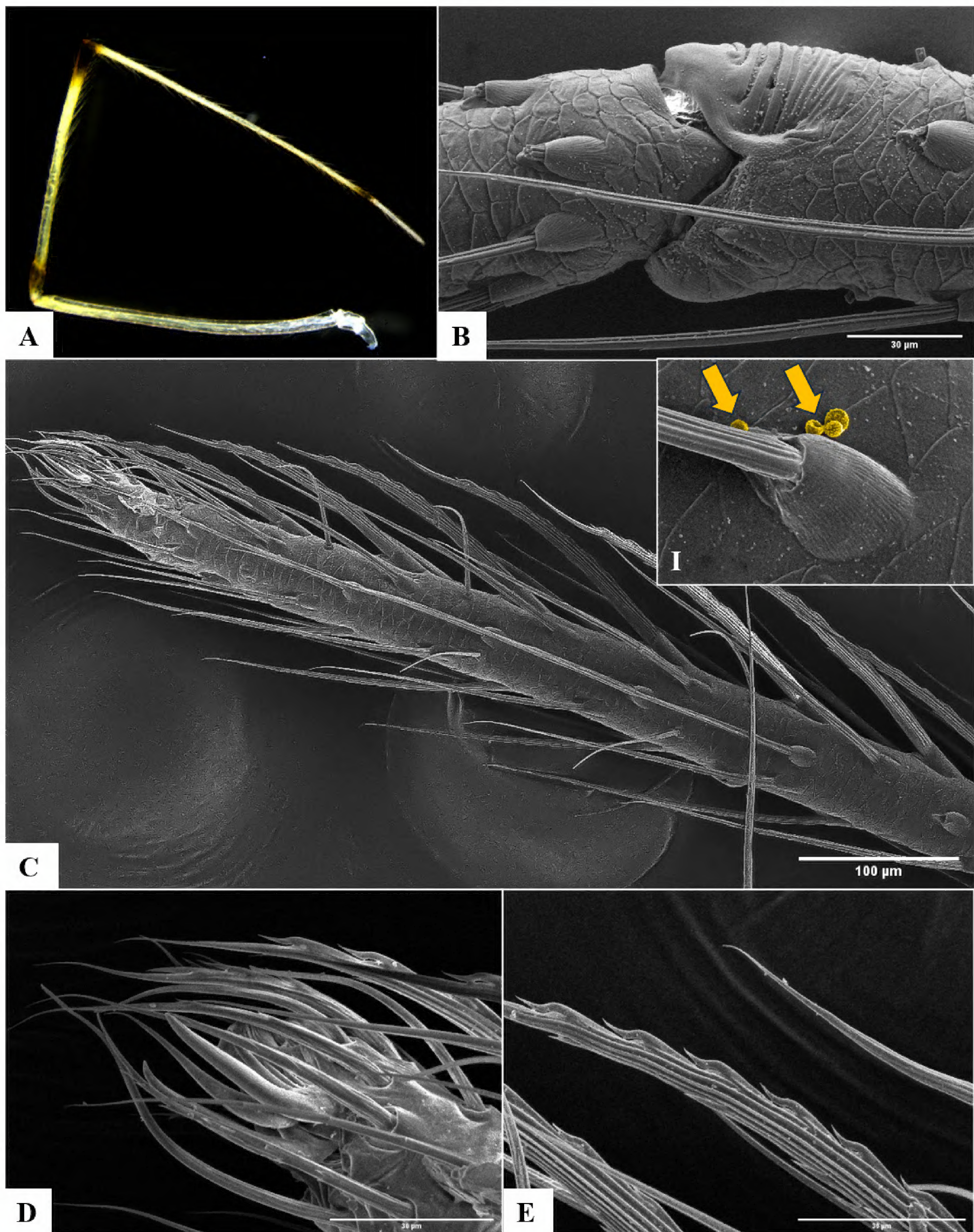


Figure 6. **A.** Showing the female leg; **B.** Showing the joint between the legs and lyriform organ (Stripe like structure next to the joint) **C.** Tarsal comb; **I.** Inset picture shows pollen grains (yellow arrows) at the base of mechanosensory sensilla **D.** Tarsal Claw; **E.** Depicts the mechanosensory setae of the tarsal comb.

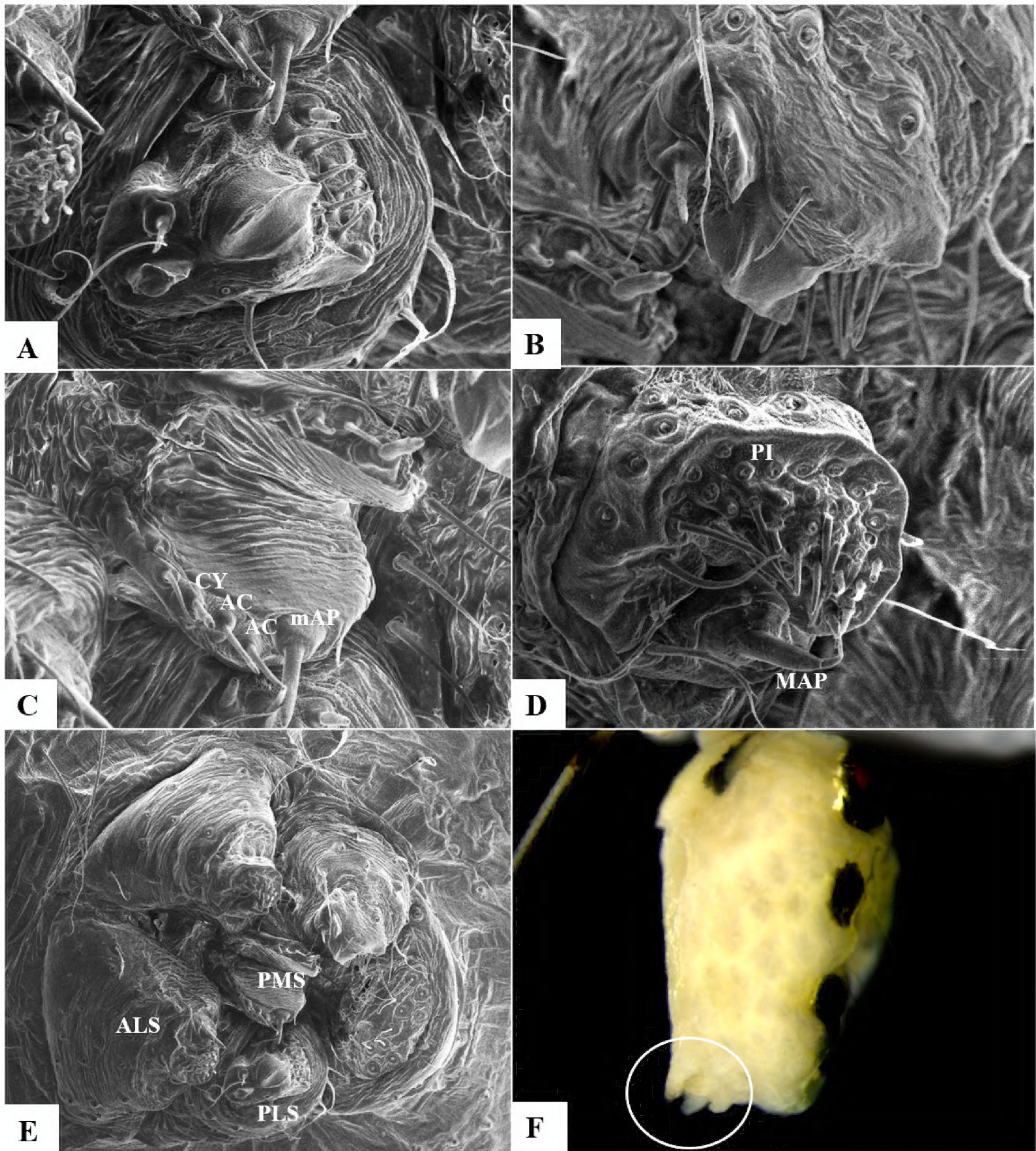


Figure 7. A–F. Spinneret; A, B. Is PLS, C. Is PMS; D. Is ALS; E. Is whole spinneret; F. Spinneret of preserved specimen.

Male (Paratype).

Measurements. Total length—2.23 mm, Carapace length—0.99mm, width—0.88mm. Abdomen length—1.24mm, width—0.52 mm, Leg I—4.01/0.42/3.27/4.84/0.92, Leg II—2.87/0.39/2.14/3.01/0.77, Leg III—1.67/0.27/1.1/1.48/0.51, Leg IV—3.23/0.36/2.45/3.48/0.74, Palp—0.64/0.16/0.16/-/0.49; Total Palp length—1.45 mm.

The description of the cephalothorax and legs of the male is similar as that of the female. The males have a smaller body but relatively longer legs and narrower abdomen (Figs 3A, 9A). The setae and eye arrangements are depicted in Fig. 10A, B.

Abdomen: In lateral view, flat from the dorsum and rounded. One red blob is segregated in the middle towards the anterior side of the abdomen, supported by a

black patch at the base. In dorsal view, four large spots, two on each side and two small at the distal end of the abdomen, are present. In some morphs only five spots are visible instead of six.

Palp: Conductor mostly membranous, folded along length, broader and chitinous apically (Fig. 9A–C). Embolus not exceeding conductor length (Fig. 9B–E), broader at base, narrow apically (Fig. 9). Tegulum and Sub Tegulum separated by thin margin (Fig. 9C).

Sensilla: The whole body, the first pair of legs, and the pedipalp of a male (*T. himalayana* sp. nov.) were used to detect the External Sense Organs (ESOs) using SEM. Six types of sensilla structures were found (Fig. 8).

Distribution. Known only from the type locality (Uttarakhand, India) (Fig. 2).

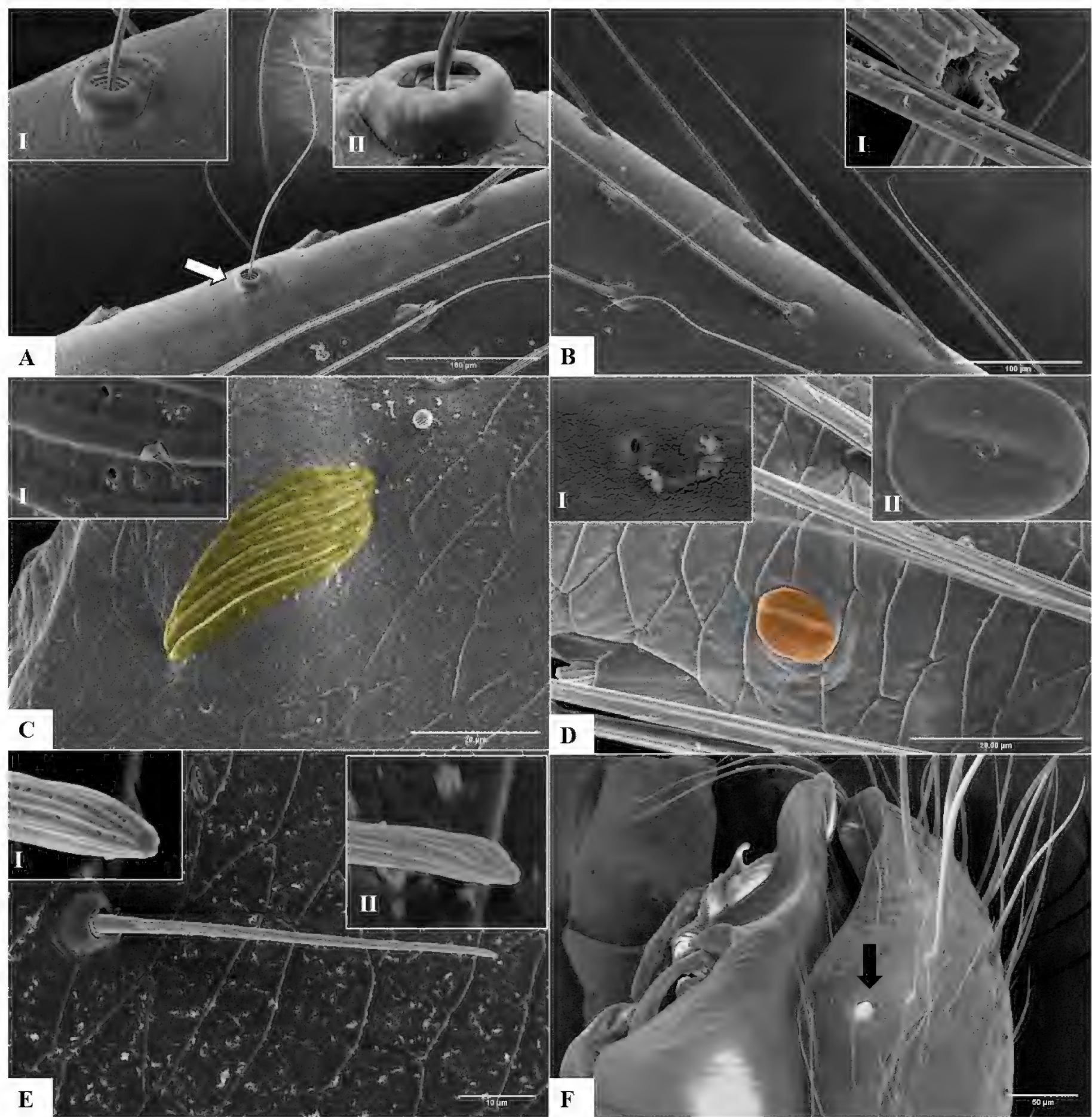


Figure 8. A–F. SEM micrographs of sensillar structures on the legs (A–E) and pedipalp (F); **A.** Trichobothria (I, II is base of the trichobothria); **B.** Mechanosensory setae; **C.** Lyriform organ (I is the pore of nerve innervation between the slits of the lyriform organ. Each slit has a single pore opening); **D.** Slit organ (‘I’ is the single pore of nerve innervation of slit sensilla); **E.** Sensilla Trichoidea (wall pore (wp) sensilla); **F.** Black arrows showing the tarsal organ on the pedipalp.

Dichotomous key to *Theridion* species of India (based on female genitalia)

- 1 Copulatory ducts (CD) very long and highly coiled; spermatheca very small; fertilization ducts (FD) relatively shorter; directed downwards with sickle-shaped tip *Theridion melanostictum*
- CD short to moderately long, not highly coiled; spermatheca normal sized 2
- 2 CD long and distinctly S-shaped, terminating in an oval loop; CD openings facing each other forming an oval loop; FD short, inclined towards each other..... *Theridion odisha*
- CD not S-shaped and not forming an oval terminal loop..... 3
- 3 CD small, slender, directed away from each other; CD shorter than spermatheca; FD short, broader at base and tapering distally, directed away from spermatheca *Theridion bengalensis*
- CD curved or short, directed downwards or converging; not slender and divergent..... 4
- 4 CD short, facing downwards without coiling; spermatheca club-shaped; CD openings directed downwards towards each other; FD small, directed upwards forming a loop..... *Theridion zonulatum*
- CD curved, protruding into hook-shaped structures facing each other and terminating parallelly downwards; CD opening located below spermatheca; FD short, directed upwards, diverging and forming a ‘V’ shape *Theridion himalayana* sp. nov.

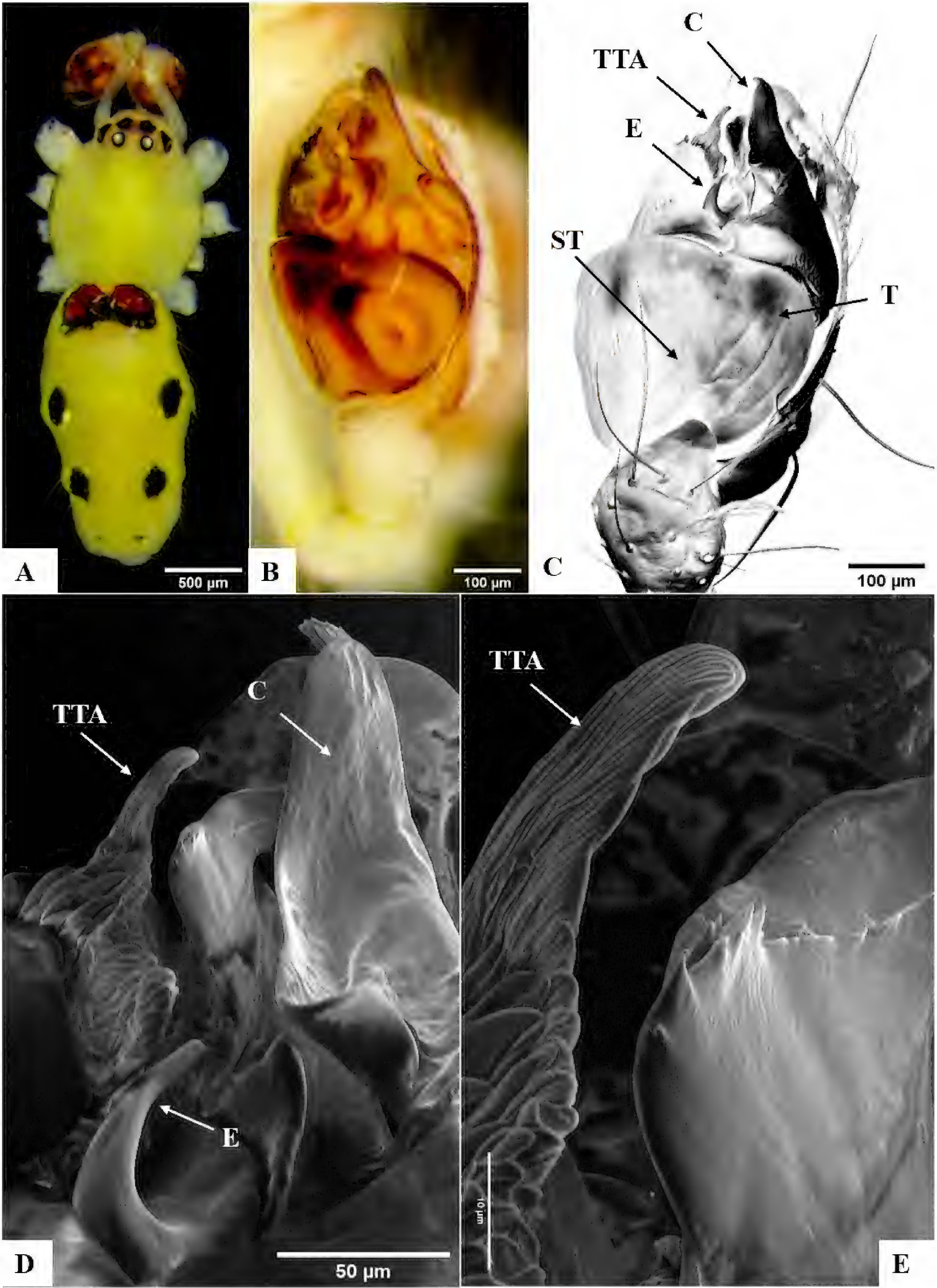


Figure 9. A. Mature male allotype of *T. himalayana* sp. nov. B–E. Pedipalp showing the E – Embolus, C – conductor, T – Tegulum, ST – Sub Tegulum, TTA – Theridion Tegular Apophysis

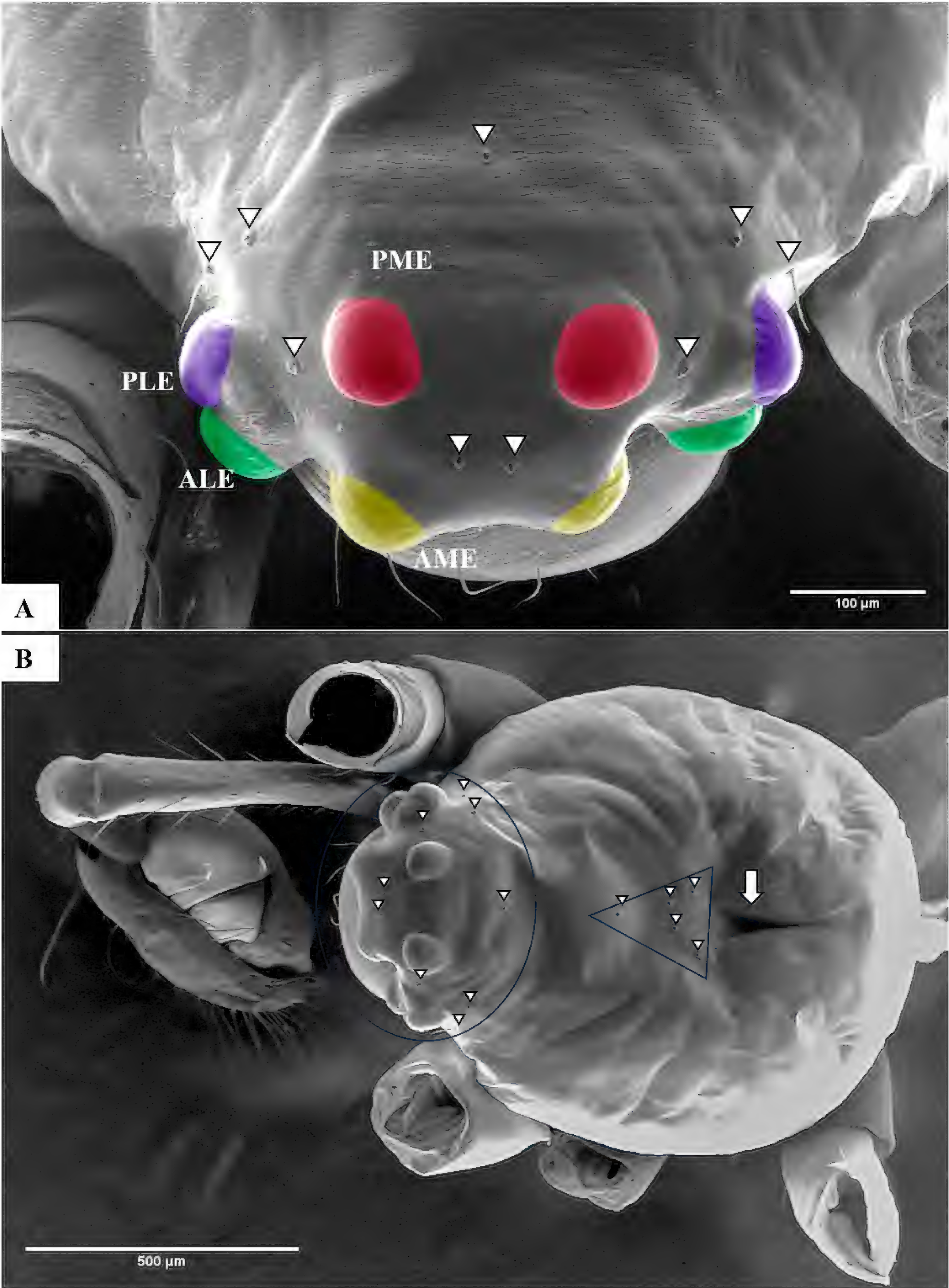


Figure 10. **A.** SEM micrographs showing the eyes and the seta arrangement of the mature male of *T. himalayana* sp. nov.; **B.** Showing the cephalothorax, pedipalp, eyes and the setae arrangement around eyes (depicted in inverted white triangles) and in the median of the cephalothorax (inverted triangle) with a fovea (white arrow).

Colour Polymorphism in *Theridion himalayana* sp. nov.

Overview of sample

A total of 61 individuals of *Theridion himalayana* sp. nov. were examined from three Himalayan sites, comprising 24 males (39.3%) and 37 females (60.7%). Five opisthosomal colour morphs were recognized: RBWR (Red Blob White Ring, 45.9%), NPB (Non-Planarian Base, 34.4%), PB (Planarian Base, 11.5%), WR (Whole Ring, 4.9%), and RBBR (Red Blob Black Ring, 3.3%), a few of which have been depicted in Fig. 15.

Sex-biased morph distribution

Colour morph frequencies showed a highly significant association with sex ($\chi^2 = 52.92$, $df = 4$, $p < 0.001$, Cramér's $V = 0.93$). Males were almost entirely NPB (87.5%, 21/24), with only rare PB (8.3%, 2/24) and RBBR (4.2%, 1/24) morphs and no RBWR or WR. Females showed a completely different pattern, being dominated by RBWR (75.7%, 28/37), with PB (13.5%, 5/37), WR (8.1%, 3/37) and RBBR (2.7%, 1/37) at lower frequencies and a complete absence of NPB. This near-complete sex-specific segregation of NPB in males and RBWR in females, together with the very large effect size, is suggestive that sex may explain most of the variance in morph distribution and could be accounted for by sex-linked genetic control, most plausibly an X-linked locus underlying the primary NPB–RBWR dichotomy. However, this needs to be tested specifically with more studies on reared populations of the spider to arrive at concrete conclusions.

Three-way interaction: sex $\times$ life stage $\times$ morph

The three-way breakdown of morph frequencies by sex and life stage showed that sex effects persist within stages. Juvenile males ($n = 5$) were predominantly NPB (80%, 4/5), with one PB individual (20%), whereas juvenile females ($n = 35$) were dominated by RBWR (77.1%, 27/35) with additional PB (11.4%, 4/35), WR (8.6%, 3/35) and a single RBBR individual (2.9%). Among mature spiders, males ($n = 19$) showed even stronger NPB dominance (89.5%, 17/19), with only one PB and one RBBR individual (5.3% each), while the two mature females comprised one RBWR and one PB individual. The fact that males and females already differ strongly in morph composition within the juvenile class (males mostly NPB vs. females mostly RBWR) suggests that if tested specifically it can be found out whether the age structure acts as an independent determinant of morph expression.

Phylogenetic relationships based on COI sequences

The maximum-likelihood (ML) analysis of 44 theridiid species (Fig. 12) recovered a generally well-resolved tree with strong nodal support (UFBoot ≥ 80 for most internal branches). The ingroup topology revealed several

genus-level clusters largely consistent with recognized taxonomic boundaries. Members of *Theridula*, *Parasteatoda*, *Rugathodes*, *Chrysso*, *Coleosoma*, and *Meotipa* each formed distinct, well-supported groups, whereas *Theridion* species were distributed across multiple clades, confirming the non-monophyly of the genus noted in previous multilocus reconstructions (Arnedo et al. 2007; Cotoras et al. 2017).

Within *Theridion*, the newly described Himalayan species *T. himalayana* clustered with *T. ohlerti* and *Coleosoma acutiventer* (UFBoot = 99; SH-aLRT = 99), forming a separate subclade distinct from the Nearctic group containing *T. californicum*, *T. frondeum*, and *T. neomexicanum*. In contrast, *T. grallator* grouped with *T. posticum* and *T. kauaiense* at the base of a separate lineage that also included *Exalbidion pallisterorum*, consistent with the earlier inference that the Hawaiian *Theridion* radiation is phylogenetically closer to *Exalbidion* than to continental *Theridion* species (Arnedo et al. 2007).

Genetic divergence

Pairwise COI distances between *T. himalayana* sp. nov. and other congeners ranged from ~0.006–0.15 (0.6–15%). The lowest divergence (0.0067) was observed with *T. saanichum*, followed by moderately low values with *T. lawrencei* (0.0505) and *T. neomexicanum* (0.0606). Divergence from *T. ohlerti*—its closest ML associate—was ~0.111, while distances to the Hawaiian *T. grallator* and *T. posticum* were 0.107 and 0.104, respectively. Comparisons with *Coleosoma* and *Meotipa* species yielded higher values (0.12–0.50), indicating deep divergence at the intergeneric level. These values fall within the typical range of interspecific COI differentiation reported for Theridiidae (Arnedo et al. 2007; Cotoras et al. 2017) and support the distinct species status of *T. himalayana*. (Suppl. material 3)

Discussion

The recent discovery of *Theridion himalayana* sp. nov. in the Western Himalayas, India adds a significant data point to the global understanding of colour polymorphism in the family Theridiidae. This is unique as it is morphologically very similar to *Theridion grallator*, while it is genetically very dissimilar as apparent from the phylogenetic studies with at least 8–12% genetic variation with different *Theridion* species. However, it would be interesting to see how the tree aligns itself when mapped with other markers as COI alone may not be telling us the entire story.

Our study documents 32 unique colour morphs in this species, matching the remarkable diversity seen in the Hawaiian happy-face spider (*Theridion grallator*) and the North American species, *Theridion californicum*. This extensive variation stands in sharp contrast to the more limited morphs in Chilean species like *Selkirkella alboguttata* (6 morphs) and *Selkirkella luisi* (2 morphs), as well as the Holarctic *Enoplognatha ovata*, which generally shows just three main forms (lineata, redimita, and ovata). While *Theridion grallator* and *Theridion californicum*

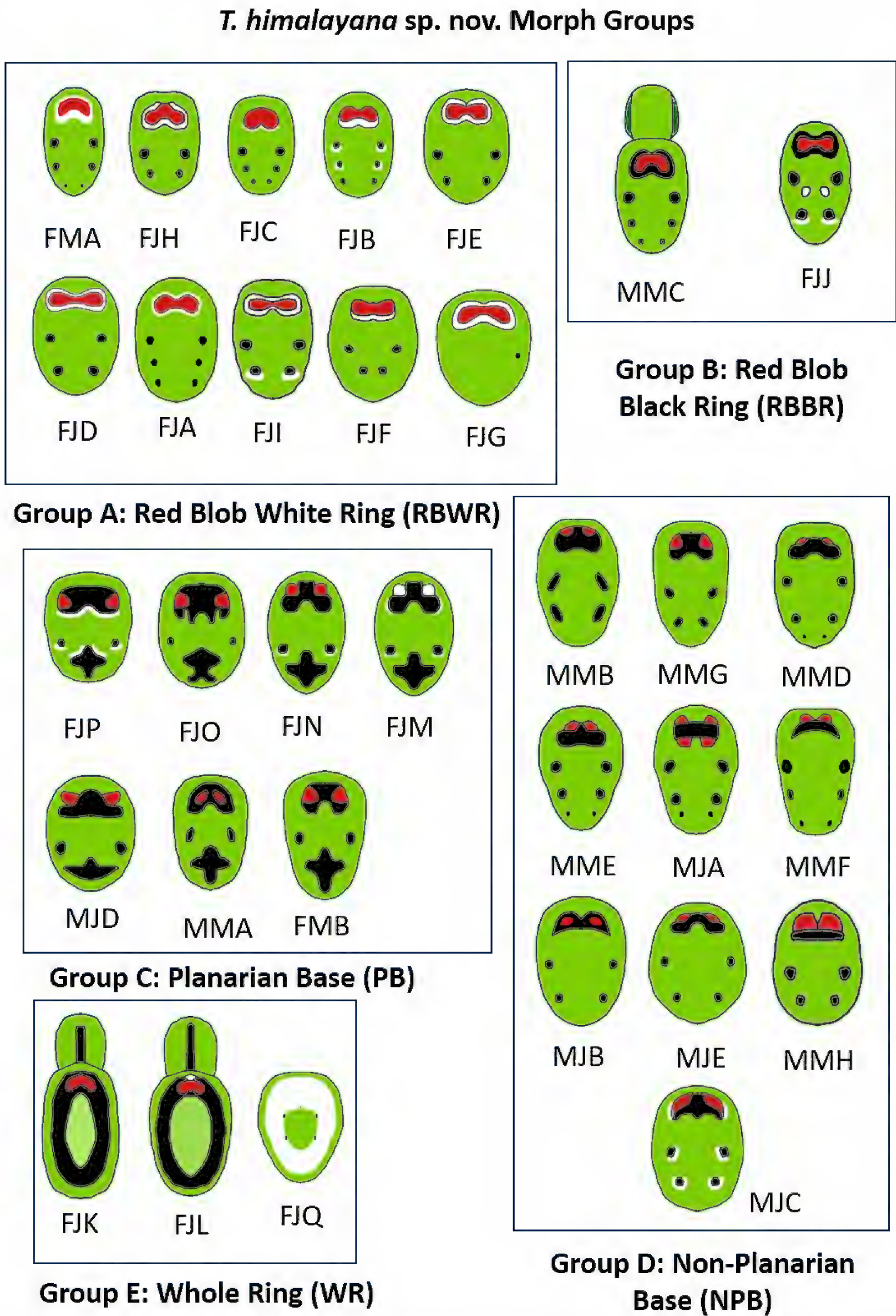


Figure 11. Collage showing morphs of all different males and females of *T. himalayana* sp. nov. in the sampled population segregated into five groups based on abdominal patterns

maintain colour morphs through autosomal Mendelian inheritance with broadly equivalent frequencies in both sexes, *T. himalayana* sp. nov. exhibits near-complete mutual exclusion of phenotypes between males and females (Cramér's $V = 0.93$, $p < 0.001$). The overwhelming prevalence of the Non-Planarian Base (NPB) morph in

males (87.5%) contrasts sharply with its complete absence in females, where the patterned Red Blob White Ring (RBWR) morph achieves 75.7% dominance. This opens possibilities for further studies to understand if the patterns are sex specific phenotypes and whether they influence expression of traits in males and females.



The pronounced sexual dimorphism of *T. himalayana* may be indicative of predation pressures experienced by each sex which can be confirmed in future investigations. It could be hypothesized that male theridiids are obligate wanderers during reproductive maturity, exposing them to intense visual predation from gleaning birds. The dominance of the NPB cryptic morph in males (87.5%) may be offering an evolutionary solution optimized for this high-risk dispersal phase through background matching against leaf undersurfaces. Adult females remain sedentary while guarding egg sacs, and the predominantly patterned RBWR morph (75.7%) may function as disruptive coloration. This hypothesis can be confirmed by rearing populations to verify the abovesaid pattern ratio and ecological roles related to sexual dimorphism and colour polymorphism.

All major polymorphic theridiid species namely *Theridion grallator* (Hawaii), *T. californicum* (California), *S. alboguttata* (Chile), and *T. himalayana* sp. nov. (India)—share specialized ecological association with leaf undersurfaces (phyllplane microhabitat), providing strong evidence for niche conservatism. This open, two-dimensional substrate exposes spiders to visual predators from above and below, creating intense selection for background-matching and disruptive coloration strategies. *T. himalayana*'s association with *Hedychium* sp. mirrors Hawaiian *T. grallator*'s use of *Broussaisia* and *Clermontia*, suggesting that leaf morphology and visual background characteristics drive convergent evolution of theridiid polymorphism. A comparative perspective reveals an evolutionary continuum: *T. grallator* and *T. californicum* exemplify classical autosomal Mendelian polymorphism; *Selkirkiella alboguttata*

represents an intermediate condition with frequency-biased sex differences (28.6% yellow males vs. 50% females); *Enoplognatha ovata* demonstrates partial sex-limitation. The *T. himalayana* sp. nov. system challenges the paradigm that theridiid colour polymorphisms are primarily maintained through apostatic selection. Instead, it may be suggestive that sex-linked genetic control enables role-specific polymorphisms wherein each sex evolves phenotypes optimized for its life history stage and ecological role, independent of population-level frequency-dependent effects. The maintenance of 32 distinct morphs despite extreme sex-linkage indicates that balancing selection continues to operate within each sex, suggesting multifactorial selection which may be hypothesised to be incorporating predation pressure, sexual selection, and ecological opportunity. Future work incorporating controlled laboratory crosses, cytogenetic analysis, transcriptomic comparisons, aviary predation experiments, microgeographic sampling, and comparative transcriptomics across *T. himalayana* sp. nov., *T. grallator*, and *T. californicum* will illuminate the mechanisms maintaining sex-linked polymorphism and the broader principles governing how sexual dimorphism, ecological specialization, and genetic architecture interact to shape the evolution of complex, polymorphic traits.

Placement of *Theridion himalayana* within Theridiidae

The Maximum Likelihood (ML) topology reinforces the view that *Theridion* as presently defined is polyphyletic, comprising several geographically and morphologically differentiated lineages. The association of *T. himalayana* with *T. ohlerti* and *Coleosoma acutiventer*, rather than with the Hawaiian or North-American *Theridion* assemblages, suggests an independent evolutionary lineage within the family. This placement is supported by the inclusion of additional theridiid genera such as *Coleosoma*, *Meotipa* and *Parastatoda* in our COI dataset (Suppl. material 1), which provides a broader comparative framework for assessing genus-level boundaries within the family. The grouping of *T. grallator* and *T. posticatum* with *Exalbidion* in a separate, well-supported clade recapitulates earlier multilocus findings (Arnedo et al. 2007) and highlights the complex evolutionary history of the Hawaiian radiation. Consequently, while *T. himalayana* shares general somatic features with other *Theridion*, its molecular distinctiveness and moderate genetic distances from both Nearctic and Pacific lineages are most consistent with its interpretation as a distinct species-level lineage within the broader theridiid radiation, rather than as a close relative of the Hawaiian assemblage.

Natural history

The species is found mainly on the abaxial side of large, broad-shaped leaves of plants namely, *Daphniphyllum himalense*, *Machilus* sp., *Cinnamomum tamala* and *Hedy-*

chium sp. found in the Himalayan moist temperate deciduous forest. The web though not significantly visible, is made using long silk strands parallel to the leaf surface and restricted to leaf undersides.

The other associated spiders found were mostly Theridiidae and Tetragnathidae spiders with similar body colour and patterns. Interestingly *T. grallator* has also been reported on *Hedychium* sp. This aspect probably suggests that the niche of this spider is specific and could reveal more answers to evolutionary questions related to coevolution and habitat specificity in two very different landscapes.

Along with the spiders, a few other organisms, like insects, amphibians, arachnids were found on and around the leaves. Some of these insects also had similar hues as on the body of the spider indicating collateral and coordinated evolutionary patterns of insects alongside arachnids to adapt to their niche on the leaf as depicted in Fig. 13A–D, indicating a probable case of Batesian or Müllerian mimicry which should be further examined to understand the prey and predator groups. On a single leaf one individual was found to nest. Nest architecture was simple and with few strands of silk woven in straight lines beneath the leaf surface as shown in Fig. 13D. Its prey were mostly dipteran flies and crane flies which were found on the web made on the underside of leaves. Mature adults were mainly found in the month of October during 2023 and 2024. Normally, the nest is made on healthy leaves, but sometimes it was also found where the leaves of *Daphniphyllum himalense* was unhealthy and infested by a gall forming psyllid (unidentified) which is possibly a food source. The spider is not aggressive or fast moving. During collection, the spider does not jump off or drop dead like other Theridiidae spiders. This species was not reported from any pitfall trap set up during the study suggesting that it has an exclusively arboreal habitat restricted to leaf undersides as was also reported in *T. californicum* and *T. grallator*.

Further it was also interesting to find that the Ginger lily (*Hedychium coronarium*) which is native to Eastern Himalayas, Bhutan, Sikkim has been introduced to the Hawaiian archipelago and has been reported to be one of the plants associated with *T. grallator* (Gillespie and Tabashnik 1994). A similar species of *Hedychium* cf. *spicatum* has been found to have been observed as the niche for *T. himalayana* sp. nov. as reported here. It will be interesting to find out in future studies as to how these plants function as microhabitat for these organisms if at all, which are not normally host specific. Further, since *Hedychium* spp. From the Zingiberaceae family is an introduced species to many parts of the world, it will be important to see if the native flora in different Indian states holds any connection with the species' distribution and presence.

The insects found in and around *T. himalayana* sp. nov. in the same habitat have also been found to show patterns of similar colours on the dorsum as seen in Fig. 14A–J. A similar pattern like that of the spider has also been reported by Gillespie et al. (1998) in other organisms. In the collage at Fig. 14, it has been recorded

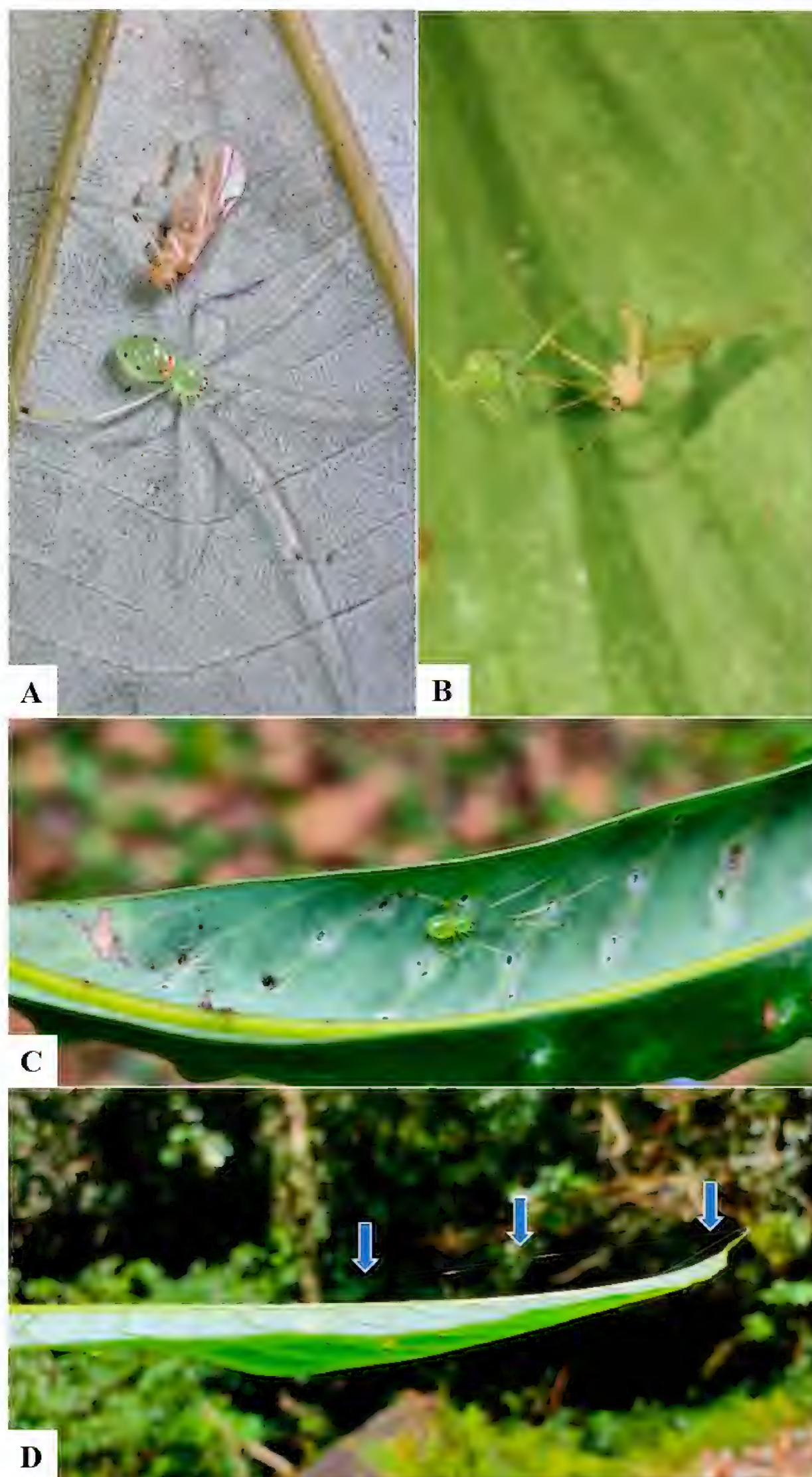


Figure 13. A, B. Showing the prey of *T. himalayana* sp. nov.; C. juvenile female resting in its nest on the Psyllid infested leaf of *Daphniphyllum himalense* leaf. D. Nest architecture of *T. himalayana* sp. nov. on the underside of the leaf.

that the animals occurring around *T. himalayana* have been strangely found to wear similar hues on the dorsum in combinations of red, green, yellow, and black. From frogs to psyllids, most animals may indicate the presence of parallel evolution in the region, but what is seen in a secluded island like Hawaii, and what other drivers trigger them towards this expression of similar colour pattern in a temperate landlocked forest at the said altitude will be interesting to find out in future studies.

Threat status

The individuals of *Theridion himalayana* sp. nov. were collected from the Himalayan Forest in the altitude range of (2000 m to 2200 m). The spiders were found close to the National Highway next to Kedarnath Wildlife Sanctuary (from Tala to Makku bend to Jagpura and in Mandal). The spiders were found in the deeper parts of the forest. However, further exploration and surveys can reveal

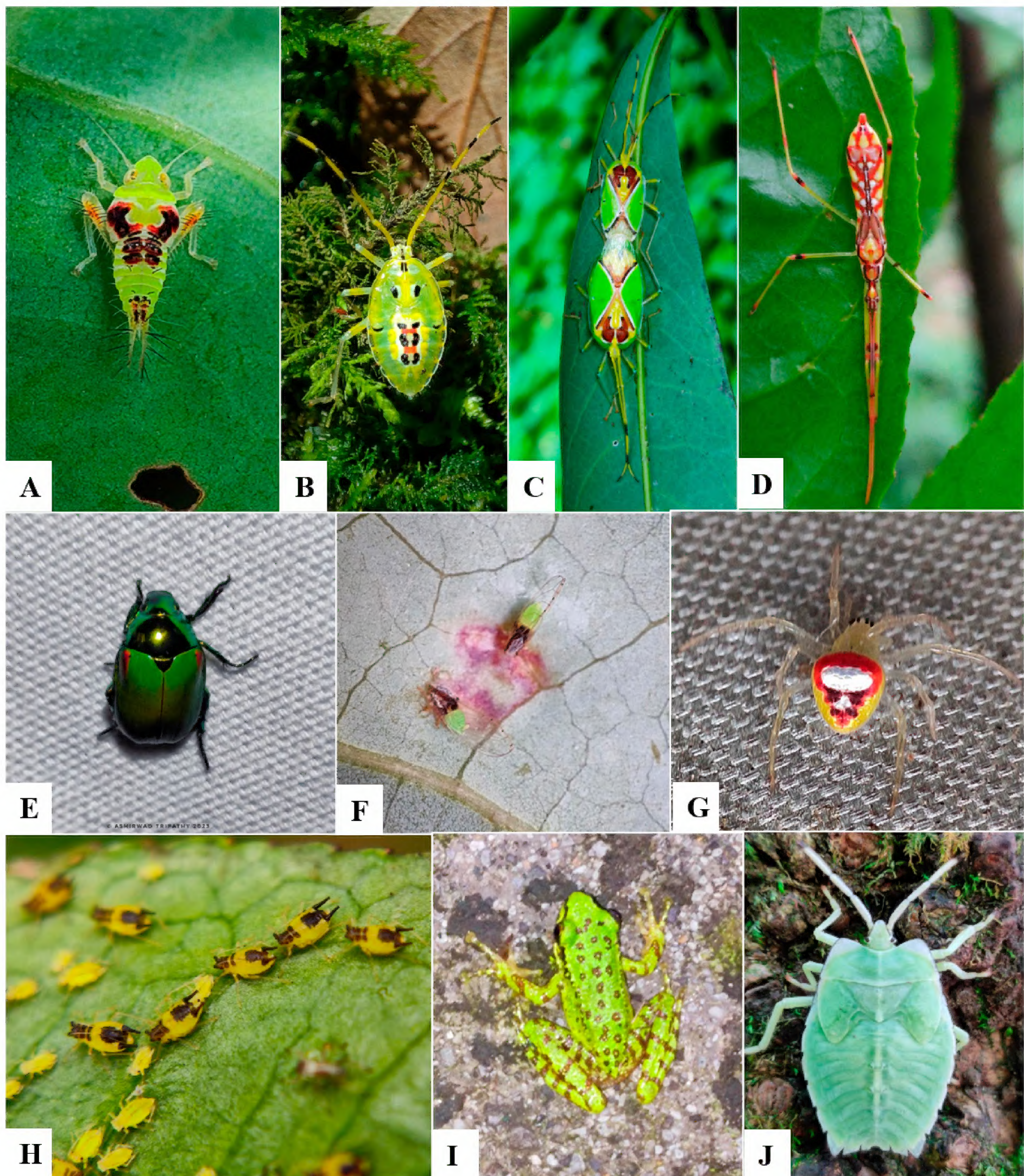


Figure 14. A. Unknown nymph of a hopper; B. *Urolabida grayii* (juvenile); C. *Urolabida grayii* (mating pair); D. Unknown Reduviidae bug nymph; E. *Callistethus stoliczkae*; F. Unknown Psyllid adults; G. *Spintharus* sp. spider; H. Unknown Aphid nymphs; I. *Amolops formosus*; J. Unknown Tessaratomidae nymph.

other potential habitats. The mature adults were found in October and appeared ready for copulation. The habitat close to the highway is mostly disturbed due to tourist movement and construction activities. Due to such factors, its population could be facing a threat and anthropogenic pressure in its habitat. If the habitat gets further disturbed due to human activities, the spiders may lose their niche and microhabitat, which they occupy amidst vegetation. Also, disturbance before October could sig-

nificantly reduce the population of this species in this forest as they are in the juvenile stage, but later in October they mostly mature, reproduce and proliferate. Egg sacs were not found during the study period. They probably lay eggs after October. The association of this species with the native flora and the threats due to habitat loss or degradation of local vegetation will be important to map noting presence and absence of the species in different seasons. Although most spiders were collected

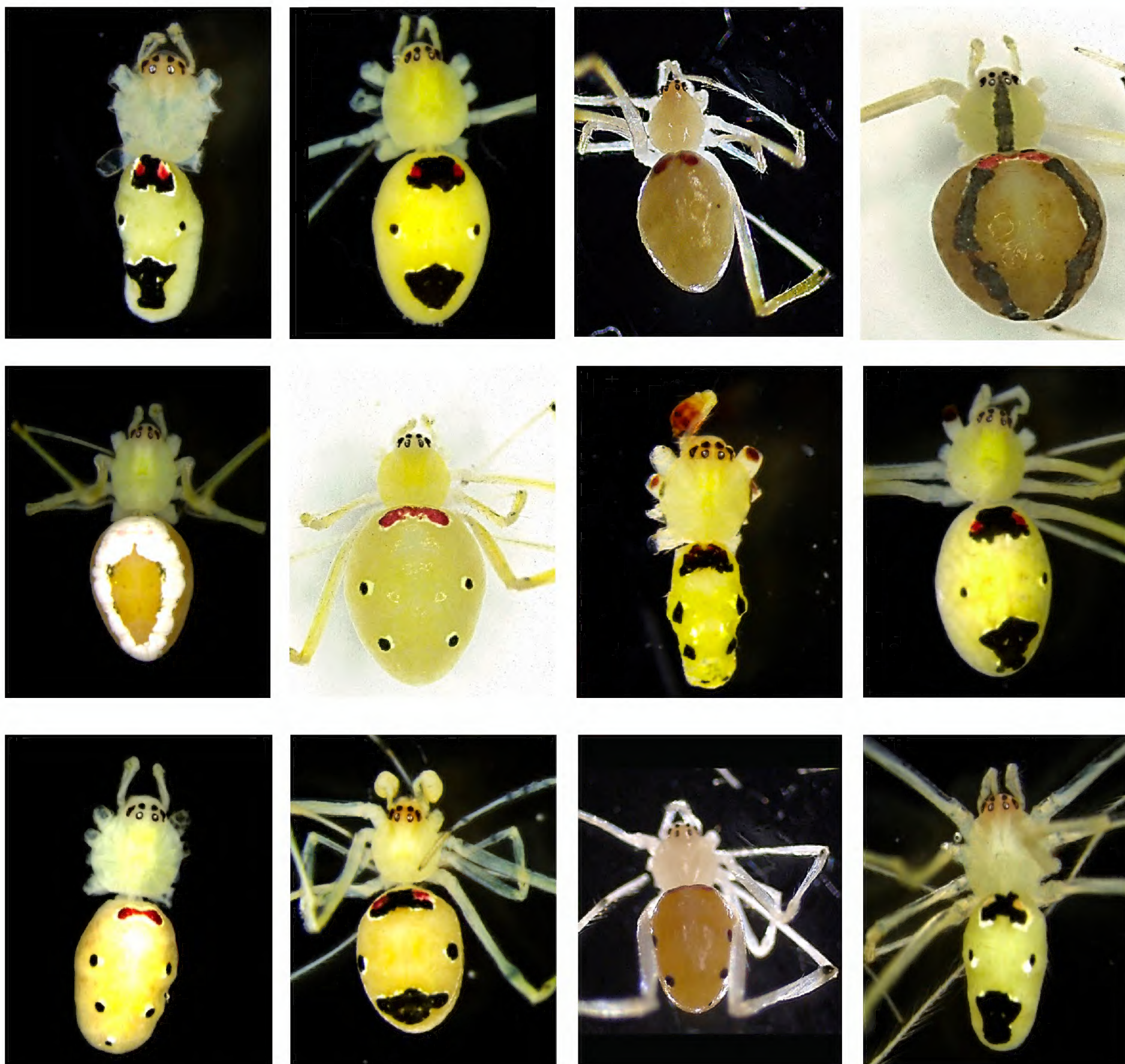


Figure 15. Collage showing morphs of some of the males and females in the population with different polymorphic patterns on abdomen.

from *Daphniphyllum himalense*, it shares a common family of plants in the Zingiberaceae family (*Hedychium* sp.) where it has been found thriving, both in the Himalayas and in Hawaii. It will be essential to understand the factors that determine this spider's microhabitat and plant preferences if any.

Conclusion

Although the present study erects the new species of *T. himalayana* that exhibits colour polymorphism with several morphs identified across males and females, it raises many evolutionary questions to be answered with further population genetics studies and specific hypotheses to be tested in order to reach concrete results. Therefore, this species presents an apt model to study polymorphism and its related hypotheses along with the

factors that drive phenotypic expression. The factors controlling polymorphism have been studied across various models and have been found to be driven by systems indicating typical patterns of convergent evolution in different landscapes across the world.

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References

- Agnarsson I (2004) Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zoological Journal of the Linnean Society* 141(4): 447–626. <https://doi.org/10.1111/j.1096-3642.2004.00120.x>
- Arnedo MA, Agnarsson I, Gillespie RG (2007) Molecular insights into the phylogenetic structure of the spider genus *Theridion* (Araneae, Theridiidae) and the origin of the Hawaiian *Theridion*-like fauna. *Zoologica Scripta* 36(4): 337–352. <https://doi.org/10.1111/j.1463-6409.2007.00280.x>
- Barret RDH, Hebert PDN (2005) Identifying arachnids through DNA sequences. *Canadian Journal Zoology* 83: 481–491.
- Cotoras DD, Brewer MS, Croucher PJP, Oxford GS, Lindberg DR, Gillespie RG (2017) Convergent evolution in the colour polymorphism of *Selkirkella* spiders (Theridiidae) from the South American temperate rainforest. *The Biological Journal of the Linnean Society* 120: 649–663. <https://doi.org/10.1111/bij.12908>
- Forster RR, Platnick NI, Coddington J (1990) A proposal and review of the spider family Synotaxidae (Araneae, Araneoidea), with notes on theridiid interrelationships. *Bulletin of the American Museum of Natural History* 193: 1–116.
- Gillespie RG, Rivera MAJ, Garb JE (1998) Sun, surf and spiders: taxonomy and phylogeography of Hawaiian Araneae. In: Seldon PA (Ed.) *Proceedings of the 17th European Colloquium of Arachnology*, Edinburgh 1997.
- Gillespie RG, Oxford GS (1998) Selection on the Color Polymorphism in Hawaiian Happy-Face Spiders: Evidence from Genetic Structure and Temporal Fluctuations on JSTOR. *Evolution* 775. <https://doi.org/10.2307/2411271>
- Gillespie RG, Tabashnik BE (1990) Maintaining a happy face: stable colour polymorphism in the spider *Theridion grallator* (Araneae, Theridiidae). *Heredity* 65(1): 67–74. <https://doi.org/10.1038/hdy.1990.71>
- Gillespie RG, Tabashnik BE (1994) Foraging behaviour of the Hawaiian Happy Face Spider (Araneae, Theridiidae). *Annals of Entomological Society of America* 87(6): 815–822. <https://doi.org/10.1093/aesa/87.6.815>
- Levi HW (1957) The spider genera *Enoplognatha*, *Theridion* and *Paidisca* in America north of Mexico (Araneae, Theridiidae). *Bulletin American Museum Natural History* 112: 1–123.
- Oxford G (1983) Genetics of colour and its regulation during development in the spider *Enoplognatha ovata* (Clerk) (Araneae: Theridiidae). *Heredity* 51: 621–634. <https://doi.org/10.1038/hdy.1983.74>
- Oxford GS, Gillespie RG (1996) The effects of genetics background on the island specific control of a colour polymorphism in *Theridion grallator* (Araneae: Theridiidae), the Hawaiian happy-face spider. *Heredity* 76: 257–266. <https://doi.org/10.1038/hdy.1996.39>
- Oxford GS (2008) An exuberant, undescribed colour polymorphism in *Theridion californicum* (Araneae, Theridiidae): implications for a theridiid pattern ground plan and the convergent evolution of visible morphs: colour polymorphism in *T. californicum*. *Biological Journal of the Linnean Society* 96: 23–34. <https://doi.org/10.1111/j.1095-8312.2008.01117.x>
- Oxford GS (2009) An exuberant, undescribed colour polymorphism in *Theridion californicum* (Araneae, Theridiidae): implications for a theridiid pattern ground plan and the convergent evolution of visible morphs. *Biological Journal of the Linnean Society* 96: 23–34. <https://doi.org/10.1111/j.1095-8312.2008.01117.x>
- Oxford GS (1985) Geographical distribution of phenotypes regulating pigmentation in the spider *Enoplognatha ovata* (Clerck) (Araneae: Theridiidae). *Heredity* 55: 37–45. <https://doi.org/10.1038/hdy.1985.69>
- Prasad P, Tyagi K, Caleb JT, Kumar V (2019) A new species of the cob web spider genus *Theridion* from India (Araneae: Theridiidae). *Ecologica Montenegrina* 26: 108–117. <https://doi.org/10.37828/em.2019.26.7>
- Simon E (1900) Arachnida. In: Sharp D (Ed.) *Fauna Hawaiiensis, or the Zoology of the Sandwich Isles: Being Results of the Explorations Instituted by the Royal Society of London Promoting Natural Knowledge and the British Association for the Advancement of Science*. Cambridge University Press: Cambridge, UK 2(5): 443–519.
- Vanuytven H (2021) The Theridiidae of the World. A key to the genera with their diagnosis and a study of the body length of all known species. *Newsletter of the Belgian Arachnological Society* 35(sup): 1–363.
- Walckenaer CA (1805) *Tableau des aran'eides ou caract'eres essentiels des tribus, genres, familles et races que renfermele genre Aranea de Linn'e, avec la d'esignation des esp'eces comprises dans chacune de ces divisions*, Paris, France.
- World Spider Catalog (2025) World Spider Catalog. Version 26. Natural History Museum Bern. <http://wsc.nmbe.ch> [accessed on 5/09/25]. <https://doi.org/10.24436/2>

Supplementary material 1

Fasta file of coi sequence of t himalayana with genbank code

Authors: Ashirwad Tripathy, Devi Priyadarshini

Data type: fa

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Supplementary material 2

Phylogenetic tree

Authors: Ashirwad Tripathy, Devi Priyadarshini

Data type: pdf

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Supplementary material 3

Pairwise COI p Distance Heat map

Authors: Ashirwad Tripathy, Devi Priyadarshini

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Supplementary material 4

Image plate depicting adult and juvenile male female spiders

Authors: Ashirwad Tripathy, Devi Priyadarshini

Data type: tif

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Supplementary material 5

Morph frequency chart

Authors: Ashirwad Tripathy, Devi Priyadarshini

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Supplementary material 6

Illustration of female morphs in *T. himalayana*

Authors: Ashirwad Tripathy, Devi Priyadarshini

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Supplementary material 7

Illustration of male morphs in *T. himlayana*

Authors: Ashirwad Tripathy, Devi Priyadarshini

Data type: tif

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